

A REASSESSMENT OF THE TYPE SPECIMENS
OF *TITANODERMA VERRUCATUM* AND *T. MACROCARPUM*
(RHODOPHYTA, CORALLINACEAE)¹

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ABSTRACT. — An historical analysis of the concept and classification of *Melobesia verrucata* Lamouroux and *M. macrocarpa* Rosanoff was made and their type specimens were examined. Both specimens showed the dorsoventral thallus construction, unistratose hypothallium composed of tall, obliquely orientated cells that were often sinuate; secondary pit connections; and single-pored tetra/bisporangial conceptacles characteristic of the genus *Titanoderma* Nägeli (syn. *Dermatolithon* Foslie). Both species have generally been subsumed in *Titanoderma pustulatum*, but examination showed that they are distinct both from this species and from each other. The principal distinguishing features were found to be the nature of the conceptacle roof surface and the anatomical structure of the roof.

RÉSUMÉ. — Une analyse historique de la conception et de la classification de *Melobesia verrucata* Lamouroux et *M. macrocarpa* Rosanoff a été faite et les spécimens type ont été examinés. Tous deux ont montré : une construction dorsoventrale du thalle; un hypothalle unistratifié, composé de hautes cellules, orientées obliquement et souvent sinueuses; des synapses secondaires; des conceptacles tétra/bisporangiaux unipores caractéristiques du genre *Titanoderma* Nägeli (syn. *Dermatolithon* Foslie). Ces deux espèces ont généralement été incluses dans le *Titanoderma pustulatum*, mais à l'examen, elles se sont montrées être distinctes de cette espèce, et constituer en outre des taxons indépendants. Le facteur principal de distinction s'est avéré être la nature de la surface du toit du conceptacle et la structure anatomique de celui-ci.

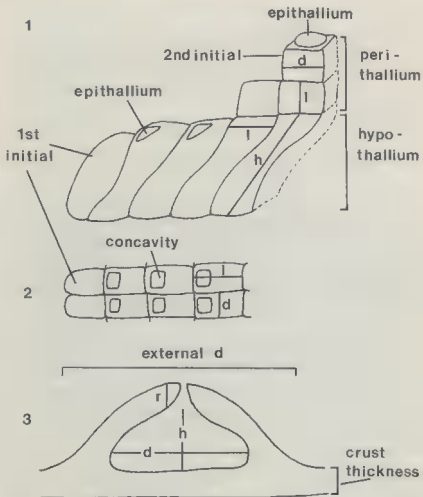
KEY WORDS : Taxonomy, Corallinaceae, *Titanoderma pustulatum*, *Titanoderma verrucatum*, *Titanoderma macrocarpum*.

INTRODUCTION

During the course of a taxonomic and nomenclatural reassessment of *Titanoderma* Nägeli (syn. *Dermatolithon* Foslie, 1898), WOELKERLING, CHAMBER-

1. Communication présentée au Colloque de la Société Phycologique de France à Caen (25-27 avril 1986), en hommage à Madame le Professeur P. GAYRAL.

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Figures 1-3. — Diagrammatic representations of *Titanoderma* thallus in VS (Fig. 1), thallus edge in surface view (Fig. 2) and conceptacle in VS (Fig. 3) to indicate thallus parts and positions at which length (l), diameter (d), height (h) and roof thickness (r) are measured in the various components.

LAIN and SILVA (1985) provided a detailed account of the generitype specimen (i. e. the type specimen of the type species) *T. pustulatum* (Lamouroux) Woelkerling, Chamberlain & Silva (Basionym: *Melobesia pustulata* Lamouroux) and also transferred 15 other species into the genus. They noted the need for further studies to clarify taxonomic limits and relationships at species level. Subsequent taxonomic investigations of *Titanoderma* in the the British Isles

have led to the conclusion that, in general, the characters on which species of this genus are usually distinguished are inadequate.

Two attempts (DAWSON, 1955; LEMOINE, 1971) to key out the species on a world-wide basis relied on characters such as presence or absence of vegetative perithallial filaments and the number of cells in those filaments (LEMOINE, 1971), and additionally cell size, conceptacle diameter and degree of prominence of conceptacles (DAWSON, 1955). Unfortunately, all these characters tend to vary within rather wide limits in most species and this has made species recognition difficult. GARBARY (1978), in a scanning electron microscope study, proposed the nature of the roof surface (i. e. stepped or not) as a significant feature and showed that *Dermatolithon litorale* (Suneson) Hamel & Lemoine had a stepped roof while *D. pustulatum* (Lamouroux) Foslie did not. This feature later proved significant also in species of *Pneophyllum* (CHAMBERLAIN, 1983) as did the anatomical structure of the conceptacle roof. SUNESON (1943, p. 41 - as *Lithophyllum*) commented similarly on the taxonomic significance of the anatomical structure of the *Titanoderma* roof. Examination of these two characters in *Titanoderma* reveals them to be of use in species' determination.

MATERIAL AND METHODS

Data were obtained from type and other historically important specimens housed at CN (Université de Caen, France), CO (Laboratoire Maritime, Concarneau, France), CHE (Société des Sciences Naturelles et Mathématiques de Cherbourg, France), L (Rijksherbarium, Leiden, Netherlands), LD (Institute of Systematic Botany, Lund, Sweden) and TRH (Kongelige Norske Videnskabers Selskabs Museet, Trondheim, Norway). Microtechnique and scanning electron microscopy technique were as in CHAMBERLAIN (1983). † indicates that a specimen has been examined by the author.

Measurement conventions are shown in Figures 1-3. It should be noted that the length (l) of hypothallial and perithallial cells relates to their position in respect to the marginal and subepithallial meristem respectively. The height of the hypothallial cell (Fig. 1) is measured obliquely across the cell, this results in the apparent anomaly that the thickness of a crust composed of hypothallium and epithallium only may be less than the height of the cells of which it is composed.

In species with a stepped conceptacle roof, the upper cell of the roof filament has a thick, calcareous cap (Fig. 10) which cradles the epithallial cell so that it comes to lie more or less at right angles to the roof surface. In species without a stepped roof, the calcareous cell walls (Fig. 11) form a ring encircling the epithallial cell which lies in the plane of the roof surface giving a honeycomb-like appearance (Fig. 11). In scanning electron micrographs of air dried material the epithallial cell usually dries out to leave a depression which is known as the epithallial concavity.

Published name	Melobesia verrucata Léodouze 1816, p.316	Melobesia pustulata & cancellata Kützing 1849, p.696	Melobesia verrucata sensu Kützing, 1849, p.696 and 1864, p.24, tab.96	Melobesia verrucata sensu Harvey, 1849, p.109 and 1851, pl. 347C	Melobesia verrucata sensu P. & M. Crozet 1860, p.4 & 1867, p.150 (on Phyllophora)	Melobesia verrucata sensu P. & M. Crozet 1860, p.4 & 1867, p. 150 (on <i>Fucus serratus</i>)
Identity of specimen on which published name was based	<i>Titanoderma verrucatum</i>	<i>Titanoderma verrucatum</i>	a foraminiferan	probably <i>Titanoderma</i> sp.	<i>Fossilifella farinosa</i>	<i>Fossilifella farinosa</i> ≠ <i>Pneophytium limitatum</i>
Areschoug, 1852	p.513 <i>M.verrucata</i>			p.513 <i>M.verrucata</i>		
Lo Jolis, 1863	p.151 <i>M.membranacea?</i>			p.151 <i>M.membranacea?</i>		
Rocanoff, 1865	p.78 <i>M.pustulata</i>	p.73 <i>M.pustulata</i>		p.66 <i>M.membranacea?</i> p.69 <i>M.farinosa</i>		
Foslie, 1906a					pp 10, 16 <i>M.farinosa</i>	pp 10, 16 <i>Densolithon</i> <i>pustulatum?</i>
Foslie, 1905	p.218 <i>M.pustulata</i>		p.118 <i>M.pustulata</i>	p.73 <i>Lichothamnion</i> <i>membranaceum?</i>	p.96 <i>M.farinosa</i> pro parte	
De Toni, 1905	p.1771 <i>D.pustulatum</i> pro parte		p.1765 <i>M.farinosa?</i>			p.1771 <i>D.pustulatum</i>
Moza, 1917	p.196 <i>M.farinosa</i> pro parte		p.196 <i>M.farinosa</i>			p.199 <i>D.pustulatum</i>
Hanel & Lecomte 1953	p.59 <i>D.pustulatum</i>				p.107 <i>M.farinosa</i> pro parte (not not specified by H & L)	
Chamberlain, 1978b	<i>D.litorale</i> pro parte					

Table 1 — To show the usage of various names connected with *Titanoderma verrucatum* (a «?» inserted when used by the author concerned)

OBSERVATIONS

Melobesia verrucata Lamouroux (1816, p. 316)

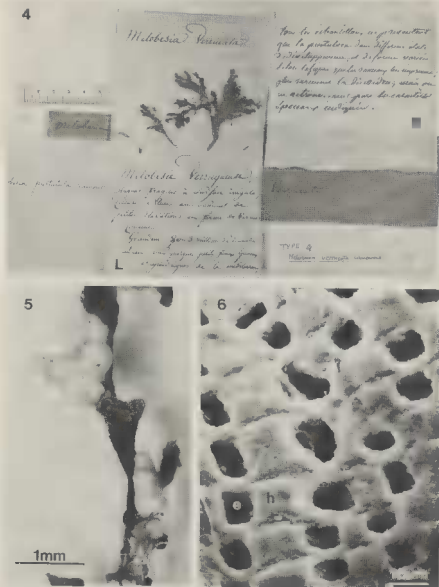
HISTORICAL BACKGROUND

The original publication of *M. verrucata* (LAMOUROUX, 1812, p. 186) was a nomen nudum, but LAMOUROUX (1816) later published a brief description of the species which he thought was a polyporous animal. Since 1816 the concept of *M. verrucata* has undergone many vicissitudes (Table I). Until now, however, the type specimen has not been re-examined nor have most of the specimens on which subsequent records were based.

Following LAMOUROUX, HARVEY (1849 and 1851, pl. 347C) recorded and figured plants growing on *Phyllophora* in Ireland as *M. verrucata*, but Harvey's specimens cannot be found and his description, while almost certainly representing *Titanoderma*, does not enable secure identification of his material. ARESCHOUX (1852, p. 513) retained *M. verrucata* Lamouroux, adding HARVEY's record and also KÜTZING's (1849, p. 696 and 1869, p. 34, tab. 96). However, examination of Kützing's specimen (L no. 940.317.498 !) shows it to be a foraminiferan, although the specimens of *M. pustulata* β *canellata* Kützing (1849, p. 696) are true *M. verrucata* (L nos 904.315.50 ! and 940.317.503 !).

The superficial resemblance of *M. verrucata*, with its delicate thallus and prominent conceptacles to *Fosliella* spp. (subfamily Mastophoroideae), led the CROUAN brothers (1860 and 1867) to identify as *M. verrucata* plants of *Fosliella farinosa* (Lamouroux) Howe growing on *Phyllophora* (CO !), and a mixture of *F. farinosa* and *Pneophyllum limitatum* (Foslie) Y. Chamberlain growing on *Fucus serratus* L. (CO !). The *Phyllophora* epiphyte led to *M. verrucata* occurring in the synonymy of *M. farinosa* (FOSLIE, 1900a, 1900b and 1905; HAMEL & LEMOINE, 1953) while the *Fucus* epiphyte was subsequently presumed to be *Dermatolithon pustulatum* (FOSLIE, 1900a and 1905; HAMEL & LEMOINE, 1953).

LE JOLIS (1863, p. 151) transferred *M. verrucata* to *M. membranacea* (Esper) Lamouroux, probably because Harvey himself remarked that the plants resembled old thalli of *M. membranacea*. ROSANOFF (1866, p. 66), also included Harvey's *M. verrucata* in *M. membranacea* although he thought (ROSANOFF, 1866, p. 69) that *M. verrucata* is «*Melob. pustulata* croissant sur un *Rhytiphloea*», furthermore he appended a note to Lamouroux's type (Fig. 4) concluding that the specimens were stages of the development of «*la pustulosa*». Further evidence that ROSANOFF considered *M. verrucata* and *M. pustulata* to be conspecific occurs in a note from Le Jolis to JOHNSON and HENSMAN (1899, p. 26) : (*M. verrucata*, Lmx.). I do not possess any specimens of the enigmatic *M. verrucata* Lamx.; and my opinion is that such a name should be suppressed. Rosanoff, a very clever and conscientious botanist, who, at my request, undertook here the study of Melobesieae, went to Caen in order to investigate the type specimens of Lamouroux's herbarium, and ascertained that the specimen labelled *M. verrucata* by Lamouroux is nothing but *M. pustulata*.

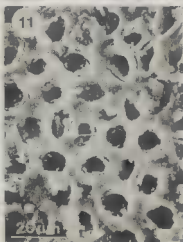
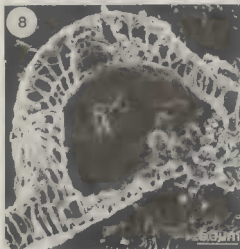
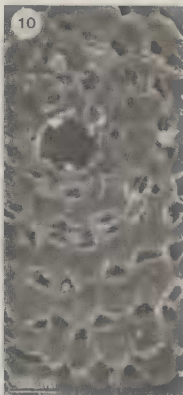
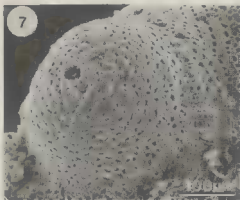


Figures 4-6. — Holotype specimen of *Titanoderma verrucatum* (= *Melobesia verrucata* Lamouroux). Figure 4, *Melobesia verrucata*, (CN), Lamouroux's handwriting (L), Rosanoff's handwriting (R). Figure 5, detail from the type. Figure 6, surface view of a crust showing hypothallial cells (h) and epithallial concavities (c).

An examination of many of the specimens at CHE cited under *M. pustulata* by ROSANOFF (1866, p. 74) shows that, for the most part they are true *Titanoderma verrucatum*, although the following taxa are also represented: *Fosliella* spp., *T. pustulatum* and *Pneophyllum limitatum*. Finally, ROSANOFF (1866, p. 73) cites «*M. canellata*» by KÜTZING (1849) as being true *M. pustulata*. Many subsequent authors have followed the practice of subsuming *M. verrucata* in *M. pustulata* including DE TONI (1905, p. 1771 pro parte - as *Dermatolithon*), HAMEL & LEMOINE (1953, p. 59, pro parte - as *Dermatolithon*) and FOSLIE (1905, p. 118 - as *Lithophyllum*).

As a result of the conflicting ideas outlined above, it is evident that the concept of a small species of *Titanoderma* corresponding to Lamouroux's *Melobesia verrucata* virtually ceased to be recognized in the early years of this century. More recently, however, a number of authors (e.g. HAMEL & LEMOINE, 1953; DAWSON, 1955; KYLIN, 1956; VAN DER BEN, 1969; LEMOINE, 1971; PARKE & DIXON, 1976; CHAMBERLAIN, 1978a, 1978b; GARBARY, 1978; CORMACI & FURNARI, 1979; CORMACI et al., 1979; BATTIATO et al., 1982; SUNESON, 1982) have recorded, as *Dermatolithon litorale* (Suneson) Hamel & Lemoine, small species of *Titanoderma* from the Mediterranean and northern Europe. SUNESON (1943, as *Lithophyllum*) based *D. litorale* on *Lithophyllum pustulatum* f. *intermedia* Foslie (1905 p. 117) and examination of both Foslie's (TRH ! and C !) and Suneson's (LD ! and personal herbarium !) material shows this species to be quite distinct from *T. verrucatum*. With regard to the above references, HAMEL and LEMOINE (1953), DAWSON (1955), KYLIN (1956) and LEMOINE (1971) base their records on SUNESON's (1943) description and are presumably not, therefore, referring to *T. verrucatum*. The references for the British Isles by PARKE and DIXON (1976), CHAMBERLAIN (1978a) and GARBARY (1978) should, however, be re-named *T. verrucatum* while the extended description (CHAMBERLAIN, 1978b) relates to a mixture of *T. verrucatum* and *D. litorale*. Finally, it is probable that the other authors mentioned above are sometimes using the name *litorale* for the ubiquitous plant correctly known as *T. verrucatum*.

To summarize, therefore, the delicate crusts with small, prominent conceptacles which characterise *T. verrucatum* have been collected extensively throughout Europe but have been confused with other taxa, in particular *Fosliella* spp., *Pneophyllum limitatum*, and other species of *Titanoderma*. This is understandable because the external morphology is very similar in all these entities, however, the characteristically oblique, sinuate hypothallial cells of *T. verrucatum* instantly distinguish this species from members of the other genera, while no other *Titanoderma* has been described to date with conceptacles as small and prominent as *T. verrucatum*. A note should be made regarding Lamouroux's unpublished species *Melobesia discoidea*. A number of specimens in Caen (!) have been labelled «*Melobesia Discoidea*» by Lamouroux; they mainly refer to calcareous epiphytes on *Padina* comprising a mixture of *Fosliella* and *T. verrucatum*. ROSANOFF (1866, p. 70) refers to *M. discoidea* in his discussion of *Melobesia farinosa* of which species he considered it to be a robust form and he



also refers to it in his annotations on Lamouroux's specimens (CN) (e.g. Fig. 4). As the name was never published it is of no further concern, but it clearly referred to a small, epiphytic entity with prominent conceptacles which included *Titanoderma verrucatum*.

DESCRIPTION OF THE HOLOTYPE (Figs. 4-10)

Titanoderma verrucatum (Lamouroux) comb. nov.

Basionym : *Melobesia verrucata* Lamouroux, 1816, p. 316.

Taxonomic synonyms : *Melobesia pustulata* β *canellata* Kützing, 1849, p. 696.

Melobesia pustulata sensu Rosanoff, 1866, p. 78, pro parte, non Lamouroux.

Further references : *Melobesia verrucata* Lamouroux, 1812, p. 186, nomen nudum

Melobesia verrucata in Areschoug, 1852, p. 513.

Excluded references : *Melobesia verrucata* sensu Kützing, 1849, p. 696; 1869, p. 34, Tab. 96, n \circ . 4397 (= a foraminiferan).

Melobesia verrucata sensu P. Crouan & H. Crouan, 1860, p. 4; 1867, p. 150 (= *Fosliella farinosa*).

Specimens : *Melobesia pustulata* β *canellata* Kützing, M. mediterr. ad *Cryptacantha squarrosa* (L 904.315.50 !); M. mediterr. in ceramio (L 940.317.503 !).

Excluded records : *Melobesia verrucata* sensu Kützing, M. Mediterran. ad Algas (L 940.317.498 !) (= a foraminiferan).

Melobesia verrucata sensu P. Crouan & H. Crouan, banc du Moulin Blanc, février 1859, sur le *Fucus serratus* (CO!) (= a mixture of *Fosliella farinosa* and *Pneophyllum limitatum*); anse du Minon, Mars 1847, sur *Phyllophora rubens* (CO!) (= *Fosliella farinosa*).

Holotype : CN ! Lamouroux, Mediterranean, on *Rytidhlaea* (Figs. 4-10).

Illustrations : CHAMBERLAIN, 1978b, pp. 297, 398 (as *D. litorale*, excl. fig. 5); GARBARY, 1978, p. 210 (as *D. litorale*).

The holotype (Figs. 4, 5) comprises fronds of *Rytidhlaea* from the Mediterranean which bear numerous, bleached plants of *T. verrucatum*. The small, delicate crusts are up to 3 mm diameter, 70 μ m thick, and often encircle the terete thallus of the host; individual crusts adhere closely to the host, adjacent crusts may overlap each other but the plants are not superimposing. Conceptacles occur frequently (Fig. 7) and are prominently hemispherical, uniporate and measure 310-350 μ m diameter. The conceptacle roof cells have prominent calcareous caps giving the roof surface a conspicuously stepped appearance (Fig. 10). The thallus forms a distinct skirt (Fig. 7) at the conceptacle base.

Figures 7-10. — Type specimen of *Titanoderma verrucatum*. Figure 7, conceptacle. Figure 8, vertical fracture through conceptacle showing clavate roof filaments (arrow). Figure 9, VS through thallus showing sinuate hypothallial cell (h) and epithallial cell (c). Figure 10, detail of conceptacle roof showing heavily capped cells (c) cradling epithallial cells (e). Figure 11, type specimen of *Melobesia pustulata* Lamouroux (CN) showing honeycomb-like surface of conceptacle roof.

In vertical section (Fig. 9) the vegetative thallus is up to c. 70 μm thick and is composed of hypothallial and epithallial cells, perithallial cells develop only in the immediate vicinity of conceptacles. Hypothallial cells are tall and sinuate (Fig. 9) and measure up to 75 μm high x 30 μm long, they have very sparse contents and are conjoined by both primary and secondary pit connections; each hypothallial cell cuts off a triangular epithallial cell (Fig. 9) which is c. 11 μm diameter. In surface view (Fig. 6) the hypothallial cells are radially elongated, 16-30 μm long x 8-16 μm wide, while the epithallial concavities are 5-10 μm long x 5-11 μm wide.

The nature of the spores in the conceptacles of the type specimen is unknown but tetrasporangial and bisporangial conceptacles have been identified in Mediterranean collections, while plants from the British Isles are always bisporangial. Internally, the hemispherical conceptacles (Fig. 8) measure about 200 μm diameter x 130 μm high, they have roof filaments (Fig. 8) which are mainly three cells deep, the central cell is relatively large and may be somewhat clavate (Fig. 8), a small epithallial cell occurs above and one, or occasionally two, more or less isodiametric cells below: these lower cells usually disintegrate as the conceptacle ages. The ostiole (Fig. 8) may be surrounded by filaments composed of three or four minute cells.

No further information is available regarding the ecology or phenology of the type material: other plants identified from Mediterranean localities occurred on terete hosts such as *Cladophora* and *Ceramium*, foliose thalli such as *Padina* and also on seagrasses. In the British Isles a similar host range is seen.

Melobesia macrocarpa Rosanoff (1866, p. 74)

HISTORICAL BACKGROUND

ROSANOFF (1866) described *Melobesia macrocarpa*, growing on *Phyllophora* at Cherbourg (CHE !) (Figs. 12, 13) as a species which resembled LA-MOUROUX's (1812) *M. pustulata*, but differed from it in having larger, more conical conceptacles and particularly in having bisporangia rather than tetrasporangia. In fact, as discussed under *T. verrucatum*, ROSANOFF's concept of *M. pustulata* mainly corresponded with *M. verrucata* Lamouroux and he considered (ROSANOFF, 1866, p. 78) that *M. verrucata* was merely a form of *M. pustulata* growing on «*Rhytiphloea*».

FOSLIE (1898, 1900a and 1904) changed his mind many times as to the affinity of *macrocarpa* before finally (FOSLIE, 1905, p. 117) concluding that it was a *Lithophyllum* of the subgenus *Dermatolithon* and that it differed from *L. pustulatum* in being a more northern form (although the type was collected at Cherbourg) while *L. pustulatum* did not occur further north than Cherbourg. In the same paper, FOSLIE also concluded that Rosanoff's original distinction between tetrasporangial *pustulatum* and bisporangial *macrocarpum* was not tenable as both types of spore occurred in both species.

Melobesia macrocarpa was recorded by ARESCHOUG (1875) growing on *Phyllophora rubens* at Warholm Island, near Gothenburg, Sweden. He described the plant as bearing large, prominent, conical, bisporangial conceptacles. Further plants from the same area, i.e. the northern Kattegat, were recorded by ROSENVINGE (1917, as *Lithophyllum macrocarpum*) although the only plant that he identified with certainty was that from Trindelen (C. Rosenvinge no. 2780 !) and no *Titanoderma* now remains on this specimen. Probably the same species as Rosenvinge's was described by SUNESON (1943) from the Swedish side of the northern Kattegat as *Lithophyllum pustulatum*; SUNESON cited *Melobesia macrocarpa* as a synonym. These plants had prominent conceptacles up to c. 600 μ m diameter and SUNESON's illustrations show roof filaments up to 6 or 7 cells long in the ostiole area; the plants were mainly bisporangial although occasional tetrasporangial ones occurred. The relationship between Suneson's and Rosanoff's plants is considered further at the end of the species' description.

LEMOINE (1913 - as *Lithophyllum*) regarded *pustulatum* and *macrocarpum* as synonymous while HAMEL and LEMOINE (1953) united the species in *Dermatolithon pustulatum* but retained the bisporangial form as f. *macrocarpa*.

Apparently no author examined the type material of either *Melobesia pustulata* or *M. macrocarpa* until WOELKERLING, CHAMBERLAIN and SILVA (1985) described the type of *M. pustulata* and showed that the conceptacles had non-stepped roofs that were in the main only three cells deep and thus differ significantly both from *M. macrocarpa* as drawn by ROSANOFF (1866, pl. IV, fig. 15) and from plants illustrated by SUNESON (1943) as *Lithophyllum pustulatum*.

In summary, therefore, the plant described as *M. macrocarpa* by ROSANOFF has usually been subsumed in *Titanoderma pustulatum* and has not, until now, been recognised as a clearly distinct species.

DESCRIPTION OF LECTOTYPE

Titanoderma macrocarpum (Rosanoff) comb. nov.

Basionym : *Melobesia macrocarpa* Rosanoff, 1866 : 74-75, pl. IV, figs. 4-8, 11-20.

Nomenclatural synonyms : *Dermatolithon pustulatum* f. *macrocarpa* (Rosanoff) Foslie, 1898 : 11.

Dermatolithon macrocarpum (Rosanoff) Foslie, 1900a : 14.

Lithophyllum macrocarpum (Rosanoff) Foslie, 1904 : 29.

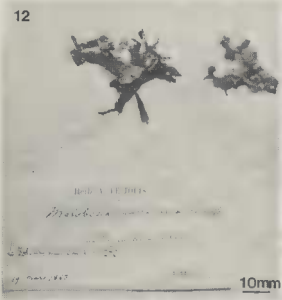
Lithophyllum pustulatum f. *macrocarpa* (Rosanoff) Foslie, 1905 : 117.

Further references : ? *Lithophyllum macrocarpum* (Rosanoff) Foslie f. *typica* Foslie; ROSENVINGE, 1917 : 263.

? *Lithophyllum pustulatum* (Lamouroux) Foslie; SUNESON, 1943 : 39-43.

Dermatolithon pustulatum f. *macrocarpa* Rosanoff, HAMEL and LEMOINE, 1953 : 70.

Excluded references : FOSLIE (1900a, 1900b, 1904 and 1905) applied the



name *macrocarpum* incorrectly to a range of plants, but in such a way that the type was always included.

Specimens : ? *Lithophyllum macrocarpum*, coll. L.K. Rosenvinge, no. 2780, Trindelen, Kattogat, Denmark, 13 July 1892, 8 fathoms on *Phyllophora membranifolia*. (C ! There is no longer any identifiable *Titanoderma* present but ROSENVINGE (1917, p. 263) considered this to be his only certainly identified specimen under this name).

? *Lithophyllum pustulatum*, coll. S. Suneson, 26 July 1938, Bohuslän : Kristineberg Sorgrundsberget, Sweden, on *Phyllophora rubens*; a further collection is dated 30 June 1949. (LD ! and in Suneson's collection !).

Excluded records : *Melobesia macrocarpa* ? coll. H.G. Simmons, Iter Faeroëne 1895 no. 6671, Insula Strömö, Thorshavn, Faeores, 9 September 1895, 1/2 - 1 m, on *Chondrus* and *Gigartina*. (LUND ! TRH !) (= *Titanoderma pustulatum* agg.).

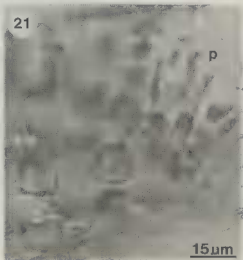
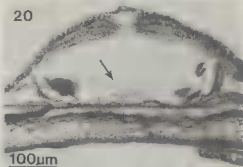
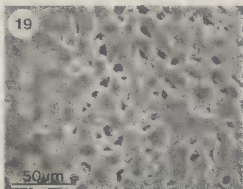
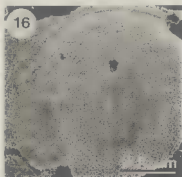
Lectotype : CHE ! Le Jolis Alg. Mar. Cherbourg no. 276, Rochers des Flamands, Cherbourg, Coll. 19 Mars 1863 on *Phyllophora rubens* (Figs. 12, 13). There are a number of isotypes in CHE.

Illustration : ROSANOFF, 1866, pl. IV, figs. 4-6, 8, 11-20 as *Melobesia macrocarpa* (see Fig. 22).

The lectotype (Fig. 12) and isotypes comprise plants of *Phyllophora rubens* (syn. *P. crispa*) which bear pink plants of *T. macrocarpum*. The smooth, flat, robust-looking crusts (Fig. 13) are up to 5 µm diameter, 100 µm thick, they adhere closely to the host and adjacent crusts overlap only slightly. Conspicuous, domed, uniporate conceptacles (Figs. 13, 16) are frequent, old conceptacles either break out or become obliterated by renewed thallus growth. The conceptacles measure 500-700 µm external diameter and have an irregularly stepped roof surface (Fig. 19).

In vertical section the thallus has a margin composed of tall, sinuate hypothallial, and triangular epithallial cells, one to three isodiametric to vertically elongated perithallial cells develop in older parts of the thallus (Fig. 15), secondary pit connections (Fig. 21) are common but cell fusions were not seen. Cell dimensions (Tab. II) are as follows : hypothallial cells 26-78 µm high x 13-19.5 µm long; perithallial cells 13-46 µm long x 8-17 µm diameter; epithallial cells c. 6.5 µm diameter. Cell contents may be sparse in younger cells and concentrated mainly at the tops of the cells (Fig. 15); older cells may contain plentiful starch grains (Fig. 15). In surface view (Fig. 14) the elongated hypo-

Figures 12-15. -- Lectotype specimen of *Titanoderma macrocarpum* (= *Melobesia macrocarpa*, Le Jolis, Alg. mar. Cherbourg no. 276 (CHE). Figure 13, detail from the type. Figure 14, surface view of a crust showing hypothallial cells (h) and epithallial concavities (e). Figure 15, VS of a crust showing hypothallial cells (h) which contain starch grains, perithallial cells (p) and epithallial cells (e).



thallial cells are 15-20 μm long x 13-18 μm diameter; epithallial concavities are 2.5 μm long x 7-12 μm diameter.

The bisporangial conceptacles (Figs. 13, 16, 17) are domed and measure 520-600 μm diameter x 190-210 μm high internally, remnants of a columella (Fig. 20) are apparent in the centre of the conceptacle floor and bisporangia, which are mainly shrivelled, occur peripherally. The roof (Figs. 17, 20, 21) is up to 100 μm deep, at the periphery the roof filaments are two to three cells long but they lengthen gradually towards the ostiole becoming up to five cells long, the ostiole itself is surrounded by small-celled filaments comprising papillae (Fig. 21). In the type material the columella remnants are quite insignificant (Fig. 20), however, ROSANOFF (1866, pl. IV, figs. 11-15; see Fig. 22) illustrated what was probably the freshly-collected material and showed abundant, apiculate, balloon-like cells forming both the columella and a lining on the under surface of the roof. Somewhat similar cells were seen in *Pneophyllum concolium* Y. Chamberlain (1983, fig. 60E) but have not been observed in other species of *Titanoderma*. On soaking, a few bisporangia (Fig. 18) swelled to possibly their original size and these measured 90-110 μm long x c. 50 μm wide.

The type plants of *T. macrocarpum* were collected in March and were reproducing abundantly with bisporangia. The plants were epiphytic on *Phyllophora* and were probably growing intertidally.

RELATIONSHIP TO OTHER RECORDS

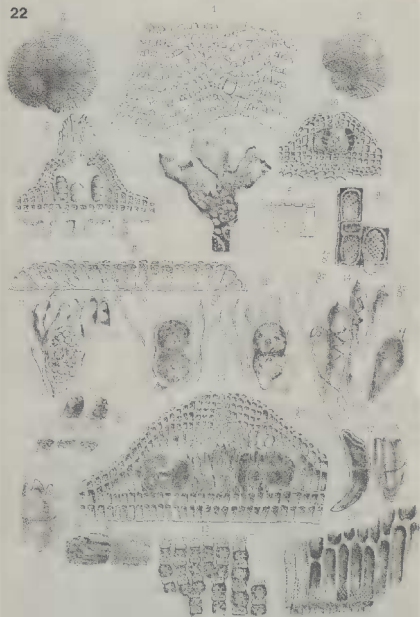
The type collection and two collections from southern England are the only firmly identified material of *T. macrocarpum*. This species and *T. pustulatum* have been somewhat indiscriminately recorded and authors have not even maintained ROSANOFF's (1866) original distinction that *T. macrocarpum* was the bisporangial form of *T. pustulatum*. The present investigation has shown that the two species are clearly distinguished on roof surface and anatomical characters and, with one exception, all examined populations subsequent to Rosanoff's that have been referred to *T. macrocarpum* have proved to belong to *T. pustulatum*. The exception is material from the waters between Sweden and Denmark referred to *Lithophyllum macrocarpum* by ROSENVINGE (1917) and *L. pustulatum* (syn. *L. macrocarpum*) by SUNESON (1943). SUNESON's description and illustrations (1943, figs. 22, 23; pl. VII, fig. 37) show that the roof is of similar structure to *T. macrocarpum* although even thicker, being up to seven

Figures 16-21. — Type specimen of *Melobesia macrocarpa*. Figure 16, Conceptacle. Figure 17, vertical fracture of conceptacle showing roof filaments (arrow) surrounding the ostiole. Figure 18, two bisporangia. Figure 19, detail of the irregularly capped roof surface with somewhat thickened cells (c). Figure 20, VS through conceptacle with remains of the balloon-like columella (arrow). Figure 21, VS of conceptacle roof filaments surrounding the ostiole, primary (1) and secondary (2) pit connections are visible, the small filaments (p) immediately round the ostiole are somewhat papillate.

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Pl. IV

22



cells deep, and the thallus and reproductive dimensions are also similar except that the bisporangia are apparently smaller in Suneson's plants. Material loaned by Dr Suneson shows epiphytic plants very similar to *T. macrocarpum* although the conceptacles are somewhat conical rather than hemispherical. Scanning electron micrographs of the roof of Suneson's plants have shown that it is stepped although differing somewhat in appearance from *T. macrocarpum* with the cells often bearing a hair base. SUNESON (1943) reports that the thallus may become up to 8 cells deep with old conceptacles becoming buried whereas Rosanoff's material is all relatively thin and conceptacles appear mainly to break out rather than become buried; these roof surface and thallus differences may simply be a question of age. The most conspicuous difference appears to be the presence of copious balloon-like cells lining the under surface of the roof and forming a prominent columella in ROSANOFF's drawing (1866, pl. IV, fig. 22) of *T. macrocarpum*. Only indistinct remnants of the columella persist in dried material but Suneson's slides and illustrations (SUNESON, 1943, fig. 22, 23) show a more or less filamentous columella and no under-roof cells which appear

Figure 22. — Plate from «Recherches anatomiques sur les Mélobésiées» by S. Rosanoff, 1866. Figs. 4-6, 8, 11-20, pertain to *Melobesia macrocarpa*. — «Fig. 4 - Frondes de *Melob. macrocarpa* (sur *Phyllophora rubens*). On voit que la plupart des frondes réniformes ont leur incisure dirigée du côté inférieur de la fronde du substratum (Grandeur naturelle). Fig. 5 - Coupe perpendiculaire au substratum d'une fronde de *Melob. macrocarpa* (Gross. de 350 diam.) Fig. 6 - Une pareille coupe, menée tangentiellement (Gross. de 350 diam.). Fig. 8 - Trois cellules frondales du *M. macrocarpa*, vues d'en haut. Leurs parois supérieures sont très nettement ponctuées. L'incrustation très forte et la couche de chaux carbonatée qui tapisse la face intérieure des cellules frondales rend leurs cavités plus ou moins arrondies. (Gross. de 1050 diam.). Fig. 11 - État jeune d'un sporange de *M. macrocarpa*, entouré des paraphyses. La cellule-mère est remplie d'un contenu incolore plein de vacuoles, et on voit le commencement de la division transversale. (Gross. de 600 diam.). Fig. 12 - État plus avancé du sporange; le contenu est coloré en rose brunâtre clair; les petites vacuoles ont disparu, et on ne voit que la disposition du contenu granuleux en réseau; dans le voisinage de la cloison, qui se forme, se trouve (dans chaque loge) une vacuole elliptique, avec un nucleus excentrique. (Gross. de 600 diam.). Fig. 13 - Un sporange, qui s'est déjà divisé en deux loges dont le contenu est granuleux et rose intense (Gross. de 600 diam.) Fig. 14 - Plusieurs paraphyses d'un cystocarpe de *Melob. macrocarpa*; leur sommet est épaissi, mamilliforme et leur contenu offre une disposition en spirale. Deux des paraphyses offrent des trous à leur sommets. (Gross. de 600 diam.). Fig. 15 - Coupe verticale et centrale d'un cystocarpe de *Melob. macrocarpa*. (Gross. de 200 diam.). Fig. 16 - a, b. Sporangies, qui commencent à s'élever du fond d'un cystocarpe. Fig. 17 - Sporangies du *M. macrocarpa*, pris dans un échantillon desséché; a - vue de face, b - vue de côté. Fig. 18 - a, b, deux sporanges de la même espèce extraits d'un échantillon desséché. Fig. 19 - Une partie de la fronde désincrustée du *M. macrocarpa*; les cellules corticales sont très apparentes. Fig. 20 - Formation des paraphyses dans le *Melob. macrocarpa*; les cloisons inclinées transversales commencent à se dédoubler, les longues cellules montrent la ponctuation régulière : a avant, et b après la désincrustation. Les cellules de la couche, qui sert de base aux futures paraphyses, ont les parois verticales très épaisses dans leur moitié inférieure et minces dans la moitié supérieure. La partie mince correspond, selon moi, à l'étendue dans laquelle s'est fait l'accroissement dans le sens vertical. (Gross. de 600 diam.).»

to distinguish his material from Rosanoff's. Further differences are the oval epithallial cells at the crust margin in SUNESON's (1943, fig. 22A) plants as compared with triangular ones in *T. macrocarpum* and the fact that this species is probably intertidal whereas Swedish material comes from the lower subtidal; both were recorded from *Phyllophora* but Suneson found plants on a variety of other hosts.

In view of the geographical separation of their localities and the noted differences in structure, it seems best to regard Rosanoff's and the Swedish plants as distinct taxa for the present, but the many similarities suggest that they may prove to belong to the variation-range of a single species.

TAXONOMIC IMPLICATIONS

This investigation shows that attempts to identify *Titanoderma* species solely on the basis of vegetative cell size and number, combined with conceptacle size,

Character		<i>T. pustulatum</i>	<i>T. verrucatum</i>	<i>T. macrocarpum</i>
maximum thallus thickness		215	70	100
perithallial cells	number	1-5	0	1-3
	l	19-40.5	-	13-46
	d	9.5-16.5	-	8-17
hypothallial cells	l	10.5-16	up to 30	13-19.5
	h	32.5-92	up to 75	26-78
tetra/ bisporangial conceptacles	roof surface	non-stepped	stepped	stepped
	external diameter	c.425	310-350	500-700
	internal diameter (d)	c.400	c.200	520-600
	internal height (h)	c.100	c.130	190-210
	number of roof cells	3	3	up to 5
	thickness of roof (r)	c.50	c.55	up to 100

Table II. - Comparative features of the type specimens of *Titanoderma pustulatum*, *T. verrucatum* and *T. macrocarpum*. (all measurements in μ m taken in vertical section).

are inadequate. The importance of the stepped or non-stepped surface and anatomical structure of the conceptacle roof have proved to be definitive in this study with respect to the three species concerned; it must, however, be recognised, in a wider context, that a combination of as many characters as possible, both quantitative and qualitative, needs to be examined in order to distinguish species of *Titanoderma*. The relevant characters for *Titanoderma pustulatum*, *T. verrucatum* and *T. macrocarpum* are summarized in Table II.

As a practical matter, *T. pustulatum* and *T. macrocarpum* are virtually indistinguishable superficially and sectioning to determine the structure of the conceptacle roof is the easiest means of identification. *Titanoderma verrucatum* may be distinguished by its small conceptacles in the present context, but examination of a wide range of European material indicates that further, similarly small species of *Titanoderma* occur and to be certain of identification, conceptacle size and structure and thallus cell sizes need to be checked.

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